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ACOUSTICAL BEHAVIOR OF THE CICADA *FIDICINA PRONOE* (WALKER)

(HOMOPTERA: CICADIDAE)

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On 4 April 1959, while descending from the cloud forests on the eastern slopes of the Sierra Madre de Oaxaca into the Valle Nacional, Oaxaca, México, I gradually became aware of a chorus of bell-like sounds above the roar of our Jeep pick-up truck. The chorus was continuous in the tropical, broad-leaved, semi-deciduous forest bordering the Río Valle Nacional along the road to Tuxtepec, Veracruz, from below Ciudad Valle Nacional (60 km roadpost) to the roadpost 50 km west of Ciudad Miguel Alemán, Veracruz. The cicadas were singing in trees and shrubs along the river and along the border of the very tall, heavy forests covering the steep slopes along the valley sides. Many of the trees on these steep hill-sides were 80 to 90 ft tall.

I stopped to tape-record the song at about the 55 km roadpost at 10:00 am, and discovered that nearby individuals did sound bell-like, but instead of the apparent two-part sound as heard from a distance above the truck's roar, the repetitious, musical phrases of their calling songs resembled the ". . . —" of "V" in Morse code, the "V's" separated by short buzzes of lower intensity. The individuals recorded were singing in the tops of trees that reached about 20 ft above the rank vegetation along the steep bank of the river. This was the approximate limit of heavy forest which descends onto the coastal and river plains. Cleared fields and orchards were scattered along the road.

The cicadas sang for at least an hour, and during this time the sky was heavily overcast—almost as dark as at dusk because of the very heavy and very low cloud cover. Between 10:30 and 11:00 am the clouds lifted, and the males rapidly dropped out of the chorus, one by one. During chorusing, individual males sang once or twice, then flew a short distance and repeated the performance. A few relatively isolated males singing in the tops of very tall trees were seen in flight between calling songs, but no females were observed flying toward them. Despite our efforts, no specimens were collected here and no nymphal skins were seen among the dense vegetation. This was the only area in which cicadas were heard singing all the way from Cd. Valle Nacional to Cd. Alemán.

About 6:30 that evening I heard the same cicada song start up suddenly at the edge of Cd. Alemán. Two small choruses of males were singing in isolated oak trees near a jai alai frontón (court) at the edge of a lime orchard bordering the Visitor's Cottage of the Comisión del Papaloapan. These trees were about 50 ft tall and relatively small at the base. I climbed one of the trees and shot 7 individuals (5 males and 2 females) that were still out of reach but silhouetted against the twilight sky. All individuals shot fell into the thick grass and other vegetation below. In the failing light, only 3 of the individuals, all males, could be retrieved.

During the last 5 min of singing activity, about 15 individuals, both males and females, flew into an area of approximately 24 ft³ where two males were the last ones singing. They were about 25 ft above the ground on the west or sunset side and near the perimeter of the crown of an isolated oak tree. Some individuals flew to this tree from smaller trees and shrubs at least 100 ft away. No noises other than calling songs were heard and no copulations were observed, although several males and females were within a few inches of each other. Here chorusing lasted from about 6:30 to 7:00 pm. beginning and ending abruptly. It seemed about as dark as 6:30 at Cd. Alemán as it had along the Río Valle Nacional at 10:00 am. On the morning and evening of March 29, and on the morning of April 5, the weather was calm, clear, and warm, and I could hear no cicadas singing in Cd. Alemán. It was evidently early in the period of adult activity, perhaps too early to expect copulation. The two locations at which I heard this species ranged from approximately 100 ft in elevation at Cd. Alemán in Veracruz to about 600 ft in the Valle Nacional in Oaxaca, and were both near tributaries of the Río Papaloapan.

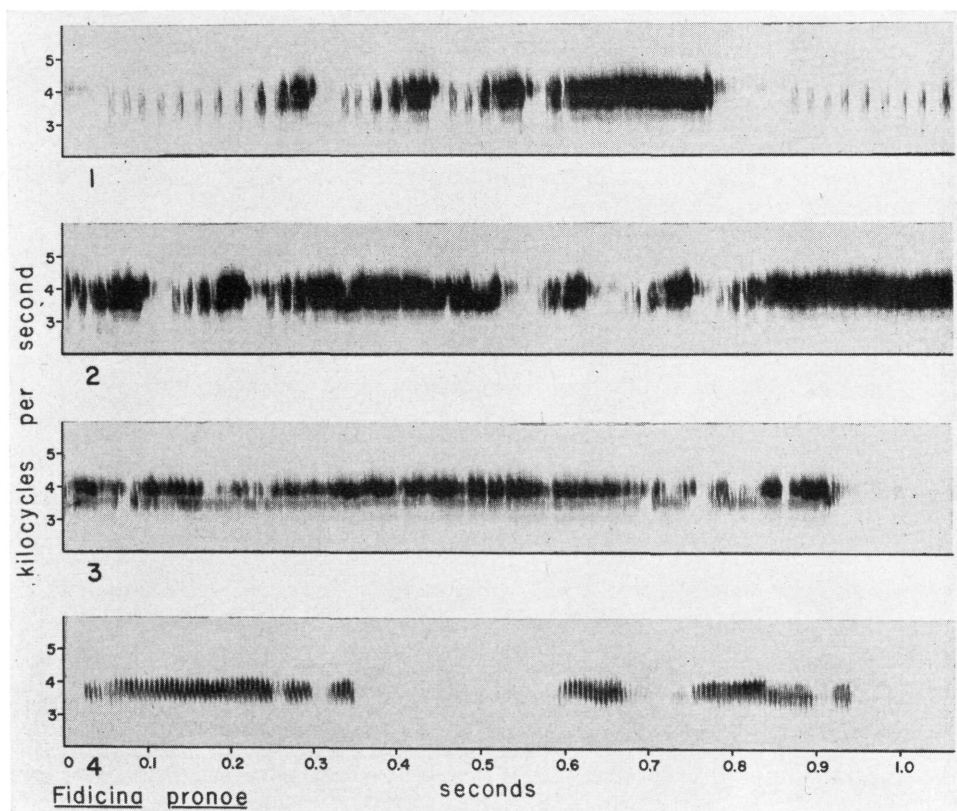
Each call has three parts: 1) a short buzz, swelling in volume, followed by 2) a series of 50 to 60 repeated units described below, and 3) a more or less continuous terminal whine lasting 4 to 5 sec. An entire call lasts about 50 to 60 sec, and gradually increases in intensity to the terminal whine. The repeated units consist of three short, musical phrases (whines), followed by a longer whine, which is followed by a short buzz containing usually 9 short phrases (fig. 1). Two or three buzzy phrases are normally produced between whines in each unit. These units are repeated at a rate of 1 to 1.5 per sec. At the end of a call only two distinct, short whines are produced, while the third is run together with the final whine of the preceding phrase (fig. 2). Figure 3 shows the concluding portion of the terminal whine of one calling song.

These calling songs were recorded at 78°F, 50 or more ft from the singing individual. No complete calling songs were tape-recorded, but one of the two recordings was of a nearly complete song (UMMZ Tape No. 543). Figure 4 shows the irregular buzzing of a disturbance squawk (UMMZ Tape No. 544), recorded at 83°F with the microphone 2 in. from a hand-held Cd. Alemán male that apparently had only wing damage after being shot with a .22 caliber dust shot load. Both calling songs and disturbance squawks contain a relatively narrow band of frequencies at about 4 kc/sec. All recordings and analyses were made with the equipment and techniques described by Moore (1961), except that an aluminum parabolic reflector 2 ft in diameter with a focal length of 6 in. (made by C. W. Torngren Co., 236 Pearl Street, Somerville 45, Massachusetts) was used in recording the calling songs.

The audiospectrographs in figures 5 to 8 are made at different analytical settings in order to show more detail of structure. It is evident from these audiospectrographs that rate and duration of timbal-muscle contraction and relaxation is the same in all types of calls. Each pulse of sound (represented by a dark vertical mark) is apparently produced by either an in- or an out-popping of the synchronized pair of timbals; the closest pairs of pulses evident in figure 8 undoubtedly represent reciprocal timbal pops. In this species, pulses produced in in- and out-pops are usually of similar intensity. Of particular interest is the fact that there appear to be two contraction rates. The complicated phrase-program of calling songs has been superimposed on one contraction rate. This rate of contraction, shown in the regular and rapid pulses of the whining parts of calling songs, indicates a timbal-muscle contraction every 0.0046 sec (220 to 230 contractions per sec) to produce 440 to 460 pulses per sec (fig. 6). At this rhythm, apparently the maximum possible at this temperature in *F. pronoe*, the intervals between contraction and relaxation and between relaxation and contraction are the same. This same rate is evident in the terminal whine (fig. 7), and in the grouped pulses of the buzzy portions of calls (fig. 5). The second

pulse rate is 340 to 350 pulses (170 to 175 contractions) per sec as seen in the irregularly produced phrases of disturbance squawks (fig. 8). Here the interval between in- and out-pops of the timbal remains the same, but the interval between timbal-muscle contractions is more variable and is increased by about $\frac{1}{3}$ (0.0054 to 0.0062 sec).

Phrase-programs involve fairly regular repetition of similar units. The consecutive buzzy phrases of the repeated units of calling songs, each containing 4 to 6 pulses (fig. 5), apparently depend on a regular delay in timbal-muscle contraction following two or three contractions at the normal rate. It is this delay,

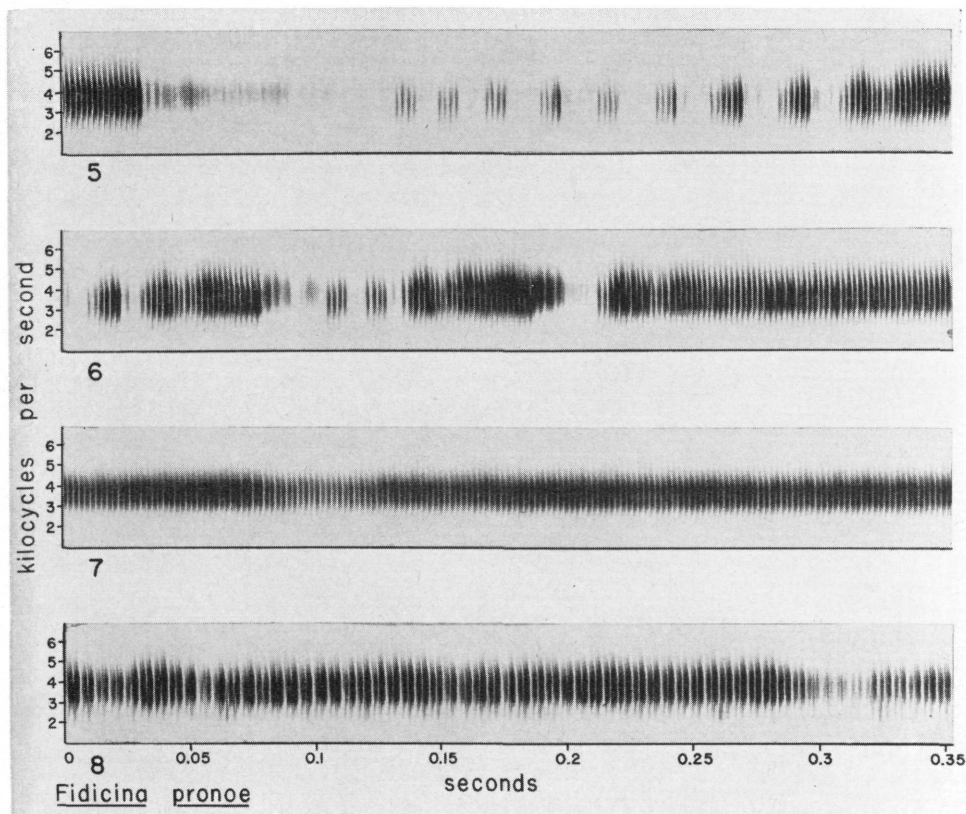


FIGURES 1 to 4, Audiospectrographs of sounds of *Fidicina pronoe*: 1) calling song, part of an early phrase; 2) calling song, beginning of the terminal whine; 3) calling song, conclusion of the terminal whine; 4) disturbance squawk. All analyses at $\frac{1}{2}$ HL BW PN (Moore, 1961).

plus the lowered intensity and the associated lowered abdominal position (changing the timbal tension and resonating properties of the abdomen), that gives the buzzy quality to this part of the call. The time-lapse between the final contraction of one buzzy phrase and the first contraction of the next varies from 0.011 to 0.019 sec, buzzy phrases being produced at this temperature at a rate of 40 to 50 per sec. Short whines contain 14 to 30 pulses and are repeated at a rate of 3.9 to 4.2 per sec, while the longer whines contain around 90 pulses and are repeated at a rate of 1.3 to 1.4 per sec in calling songs. The phrases of disturbance squawks are quite irregular in duration and in repetition rate.

The bell-like effect of portions of the calls of *Fidicina pronoe* is apparently caused by sudden beginning and ending of intense multi-pulse phrases with a narrow band of frequencies. Pringle (1954) described the song of the Ceylonese cicada *Purana campanula* as bell-like, and discussed in some detail the factors responsible for its quality.

The intense whine-like portions of calling songs are accompanied by a raising of the abdomen, as has been described for other cicadas (Pringle, 1954). The control of rhythm, intensity, and quality depends upon the interaction between

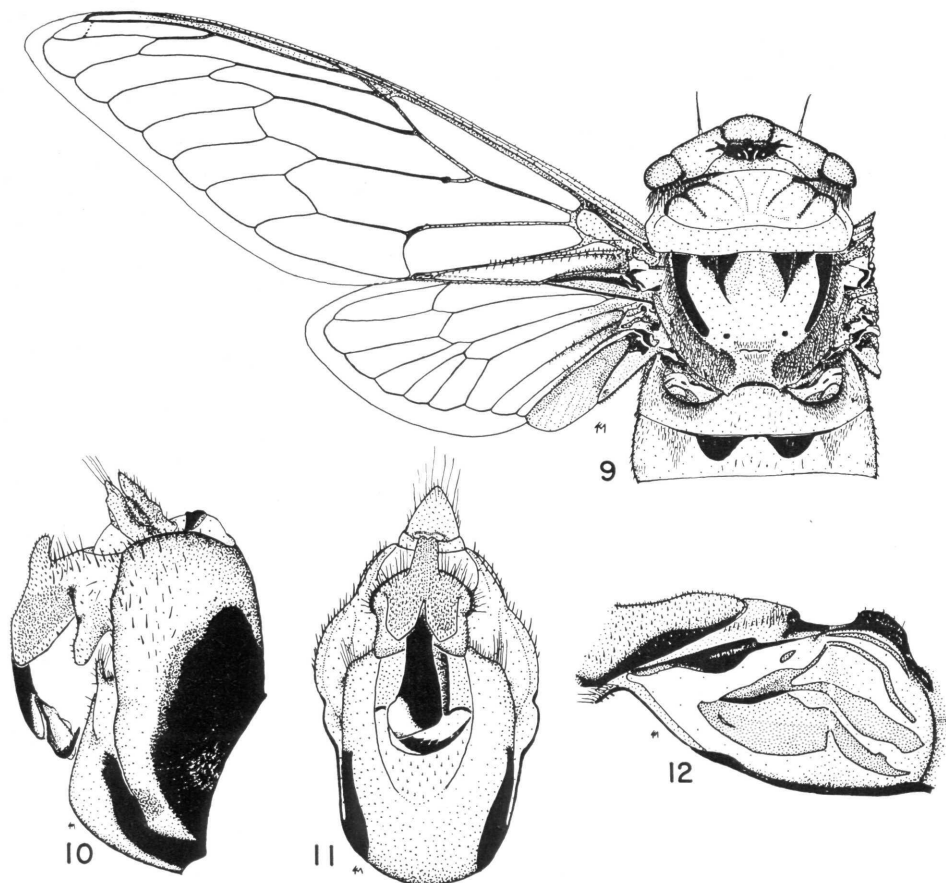


FIGURES 5 to 8, Audiospectrographs of sounds of *Fidicina pronoe*: 5) calling song, part of an early phrase; 6) calling song, part of an early phrase; 7) calling song, part of terminal whine; 8) disturbance squawk. All analyses at $\frac{1}{2}$ HH BW PX.

the central nervous system and a poorly-understood complex of muscles that controls: 1) timbal contractions, 2) shape, position, and resonance of the abdomen and its tracheal air sacs, and 3) tension of the associated timbals, tympana, and folded membrane (Pringle, 1954). The relatively low rate of repetition of phrases suggests that these may be under central nervous control, while the timbal-muscle contraction rate suggests that timbal vibration may be under myogenic control (Bullock, 1961). Voskresenskaya and Svidersky (1961) have suggested a neurogenic control of "high-frequency" muscles in insects involving frequent rhythmic reactions in which the sympathetic nervous system participates.

Fidicina pronoe is a relatively large cicada with contrasting green and black markings (fig. 9). In males, the body length is about 34 mm and the forewing length is approximately 43 mm. The configuration of the tenth abdominal segment (fig. 10 to 11), especially the caudal protuberance and the very short, stout setae on the caudo-ventral surface, and the form of the aedeagal apex shown in the same figures are diagnostic. The right timbal of *F. pronoe* is shown in fig. 12; the shape and position of its sclerotized ribs are diagnostic.

In our collection there are several specimens from other localities in México, Guatemala, Colombia, and Costa Rica which closely resemble the Cd. Alemán specimens in size, coloration, and structure of the tympana. However, there are



FIGURES 9 TO 12, Structures of *Fidicina pronoe*: 9) male, dorsal view of anterior portion; 10) ninth and tenth abdominal segments and aedeagus, lateral view; 11) ninth and tenth abdominal segments, caudal view; 12) right timbal, posterior view, timbal cover removed.

slight differences in the structure of the ninth and tenth abdominal segments, the aedeagus, and the timbals. One series of specimens from near Arriaga in Chiapas, México, was so similar morphologically that I would have assumed it to be conspecific with *F. pronoe* were it not for the following notes made by Dr. I. J. Cantrall at the time of collecting: "... sings with a coarse, ... hollow, tone—as tee zeee, tee zeee—each expression is given louder and louder until the insect sings a

continuous, ringing, but hollow zeee." This description would fit my first impression of *F. pronoe* singing in the distance as heard over the truck's roar, but is not at all similar to its four-part, Morse code-like "V" which is readily distinguished at close range (as Cantrall was when collecting the specimens). In the light of the importance of calling songs as specific aggregating mechanisms in cicadas (Alexander and Moore, 1958), these Arriaga specimens and those examined from other localities in México and Central and South America most likely represent other species, albeit very similar siblings, whose description is best left until verification of specific identity can be made from field studies of the interactions and acoustical behavior of these populations in nature.

F. pronoe has previously been reported from numerous localities in surprisingly remote regions by several authors. Walker (1850) described the species without locality, and later (1858) described *Cicada* (= *Fidicina*) *compacta*, also without locality. Stål (1854) described *Fidicina vinula* from Brazil, which he later (1862) synonymized, along with Walker's *F. compacta*, under *F. pronoe*. Distant (1881) listed in addition México, Guatemala, Costa Rica, Panama, Colombia, Trinidad, and Brazil. Uhler (1892) added Cordova and Orizaba, Veracruz, Mexico, and Southern Texas, U.S.A. This latter "soiled specimen," which "seems to belong to this species," is most likely *Tibicen superba*, a common, green, similar-appearing, summer species in Texas. *F. pronoe* in southern Texas would be several hundred miles north of the northernmost record for any other specimens of what has been called "*pronoe*." Gibson and Carrillo (1959) listed only Cotaxtla, Ver., México, for *F. pronoe*. As there is no type locality for Walker's *F. pronoe*, and as Mr. Izzard (in litt.) feels that the figures of dorsal coloration and of structure of the ninth and tenth abdominal segments and aedeagus presented here agree with Walker's type specimen, I am applying the name *F. pronoe* to the specimens recorded and collected in Oaxaca and Veracruz near confluents of the Río Papaloapan until such time as specimens of another species which more closely resembles the type are found. My drawings were made from specimens preserved in 70 percent ethyl alcohol, and the posterior view of the right timbal (fig. 12) apparently does not resemble very closely what can be seen of the partially concealed, and perhaps damaged, timbal of the pinned type (Izzard, in litt.).

SUMMARY

Males of this green tropical cicada sing primarily at dusk and during other periods of low light intensity. The ringing musical phrases of males suggest the "... —" of "V" in Morse code, while distant songs sound very much like the two-part peals of small, hand-shaken bells. Of special interest are the two rates of timbal-muscle contraction, one common to all calling song phrases (220 to 230 per sec), and the other found in disturbance squawks (170 to 175 per sec). At the end of twilight chorusing males and females fly into close proximity to the last males to stop calling. What has been called one species, *F. pronoe*, is probably a complex of several species extending from central Mexico into northern South America. This anomaly can only be unraveled through analysis of distribution and of acoustical behavior of populations through field studies.

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